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The Representation of Time for Motor Learning

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Summary

We have identified factors that control precise motor timing by studying learning in smooth pursuit eye movements. Monkeys tracked a target that moved horizontally for a fixed time interval before changing direction through the addition of a vertical component of motion. After repeated presentations of the same target trajectory, infrequent probe trials of purely horizontal target motion evoked a vertical eye movement around the time when the change in target direction would have occurred. The pursuit system timed the vertical eye movement by keeping track of the duration of horizontal target motion and by measuring the distance the target traveled before changing direction, but not by learning the position in space where the target changed direction. We conclude that high temporal precision in motor output relies on multiple signals whose contributions to timing vary according to task requirements.

Introduction

Precise timing is at the heart of all our movements. Timing on a scale of tens to hundreds of milliseconds is essential to coordinate the components of complex movements and the sequence of muscular contractions for simple movements. To achieve movements with high temporal precision, the brain must garner temporal information from internal and/or external cues and generate an internal representation of the passage of time with millisecond accuracy.

Motor timing has been examined using a variety of tasks that can be categorized according to the nature of the signals that contribute to the underlying representation of time. In some tasks, the only temporal signal available is the passage of time itself, and under these conditions timing is said to be "explicit," as if the brain were keeping track of time with a stopwatch (Buonomano and Karmarkar, 2002; Gibbon et al., 1997; Ivry, 1996; Miall, 1992; Schoner, 2002). For example, it has been suggested that maintaining an internal tempo in any solo music performance depends on a neural clock that ticks at an abstract level and provides explicit temporal reference points (Janata and Grafton, 2003; Palmer, 1997). However, temporal information is not always encoded explicitly; in some behaviors the passage of time is a derived quantity that is computed from one or more motion variables (Regan and Gray, 2000; Tresilian, 1999). For example, in tasks involving interactions with moving objects, such as catching or hitting a ball, precise timing is accomplished by deriving the time-to-arrival of the incoming object from variables that the senses can measure, such as the speed, distance, or looming of the object (Land and McLeod, 2000; Rushton and Wann, 1999).

Most real-life situations offer a wide range of signals and cues that provide temporal information and could, at least in principle, be used to achieve precise timing in our movements. Are all available signals with temporal structure used for motor timing, and if not, what determines whether any individual signal contributes to our internal representation of time? Is the contribution of any given signal fixed for a particular motor task, or can task requirements bias the way in which the brain keeps track of the passage of time?

In the present paper, we examine the signals used by the brain to achieve precise timing in the learning of smooth pursuit eye movements. Pursuit eye movements, which are used by primates to track slowly moving objects, are subject to learning. Several hundred repetitions of a consistent change in the direction or speed of motion of a visual target leads to a learned eye movement that is present even in probe trials where the change in target motion does not occur (Boman and Hotson, 1992; Fukushima et al., 1996; Kahlon and Lisberger, 1996). We now report that pursuit learning is temporally specific: the peak velocity of the learned eye movement in probe trials always occurred around the time when the target would have changed direction in the learning trials. We also demonstrate that the timing of the learned eye movement was controlled by signals that varied according to task requirements, ensuring high temporal precision under a variety of behavioral circumstances.

Results

Directional Learning of Smooth Pursuit Eye Movements

To assess the control eye movement responses, each daily experiment began with a baseline block that included approximately 50 trials of horizontal target motion at 10°/s in the learning direction (Figure 1A). In the subsequent block of learning trials, targets moved in the learning direction at 10°/s for a fixed duration before changing direction through the addition of a component of vertical motion at 30°/s for 500 ms. In Figure 1B, for example, the learning direction was rightward and a 500 ms interstimulus interval (ISI) intervened between the onset of horizontal target motion and the addition of vertical target motion. During the first few learning trials, and due to the intrinsic delay of the pursuit system (Lisberger et al., 1987), the monkeys responded to the change in target direction about 100 ms after the onset of vertical target motion. Responses after the change

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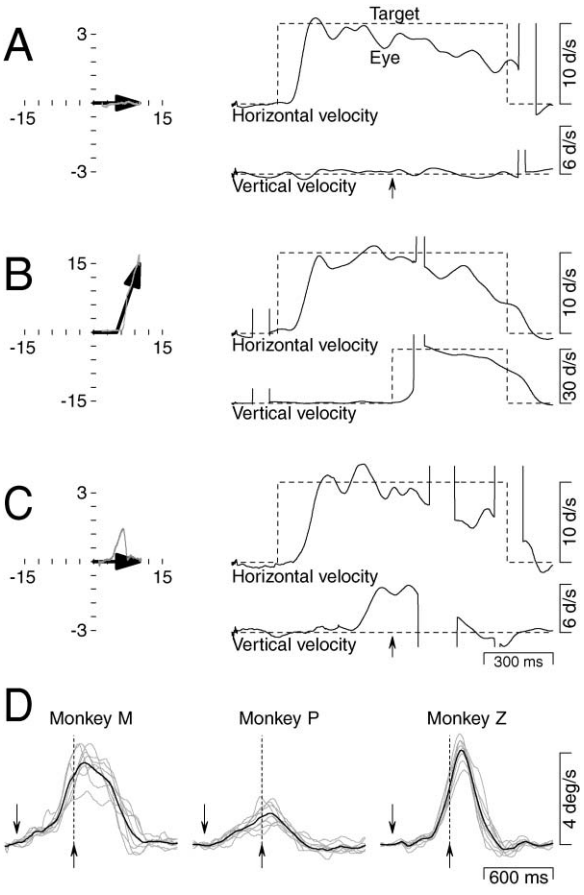

Figure 1. Trial Configurations for Directional Learning of Smooth Pursuit Eye Movements

(A) Prelearning probe trial. (B) Learning trial. (C) Postlearning probe trial. In (A)–(C), the icons at the left of each panel show the stimulus and response in terms of horizontal and vertical position. The bold, black arrow shows target motion, and the fine gray line shows the sequence of eye positions. The right side of each panel shows superimposed continuous and dashed traces for eye and target velocity, respectively; top and bottom pairs of traces in each panel show horizontal and vertical velocities. In (A) and (C), the target motion is purely horizontal, but the time when the target would have changed direction in the learning trials is indicated by the upward vertical arrows. In (B), a 500 ms pulse of vertical target velocity begins 500 ms after the onset of horizontal target motion. Note that the scale in (B) is different from (A) and (C). (D) Gray traces show the average learned vertical eye velocity in individual daily experiments; black traces show grand averages across all experiments. Downward vertical arrows show the time of onset of horizontal target motion. Upward vertical arrows and vertical dashed lines show the time of the change in the direction of target motion in the learning trials.

in direction consisted of a small smooth eye movement, a saccade to catch up with the moving target, and postsaccadic vertical eye speed that nearly matched vertical target speed (bottom panel in right side of Figure 1B). To assess any learning effects, probe trials were presented occasionally, randomly interleaved among learning trials. After 50 to 100 learning trials, the postlearning probe trials, which were identical to the trials in the baseline block and therefore consisted of purely horizontal target motion at 10°/s, evoked a horizontal smooth eye movement followed by a vertical smooth eye movement. In Figure 1C, for example, the monkey's initial rightward pursuit (top panel in right side of Figure 1C) was accompanied by a later upward smooth eye motion (bottom panel in right side of Figure 1C), even though the probe target moved only to the right. The peak of the learned vertical eye movement was timed appropriately to correspond to the time when the target would have begun to move upward on the learning trials (indicated by the upward arrow in Figure 1C).

Figure 1D shows that directional learning caused similar trajectories of learned eye movements in all three monkeys we studied. For targets that changed direction 500 ms after motion onset, the peak vertical velocity of the learned eye movement varied from about 2°/s in monkey P to about 4°/s in monkeys M and Z, but the time course was similar. The onset of the learned eye movement anticipated the onset of vertical target motion and reached a peak at about the time the vertical target motion would have begun in the learning trials (upward vertical arrows in Figure 1D).

Temporal Specificity of Learning

Altering the time when the target changed direction in learning trials changed the timing of the learned eye movement. In this set of experiments, the ISI used for the learning trials was kept constant for the whole daily session but was varied from one day to the next. We used ISIs of 50, 150, 250, 500, 750, or 1000 ms on different days. Figures 2A and 2B show two features of the learned vertical eye velocities measured in probe trials that were randomly interleaved among learning trials of a particular ISI (ISI is color coded by the downward arrows). First, the timing of the learned eye movement depended on the timing of the vertical target motion in the learning trials. The learned eye movement anticipated the onset of vertical target motion and peaked near the time when vertical target motion would have begun (Figures 2A and 2B). Second, the amplitude of the learned eye movement depended on the timing of the change in target direction. The learned vertical eye velocity was largest when, in the learning trials, the target changed direction 150 or 250 ms after the onset of horizontal target motion (red and black traces). The learned vertical eye velocity was smaller for both shorter and longer values of ISI.

Averaging across several daily experiments at each ISI revealed that, for values of ISI in the range from 250 to 1000 ms, the peak vertical velocity of the learned eye movement occurred approximately 50–100 ms after the change in direction of target motion would have occured in the learning trials (Figure 2C). When the ISI was 50 or 150 ms, the time to the peak of the learned vertical eye velocity reached a minimum at about 250 ms after the onset of the horizontal target motion, reflecting the intrinsic delay of 100 ms in the pursuit system (Lisberger et al., 1987) and the dynamics of smooth tracking eye movements. The temporal precision of the learned response also was related to the ISI used in the learning trials. The standard deviation of the time of the peak vertical eye velocity was small when the ISI was 150 ms and increased to values in excess of 300 ms when ISI

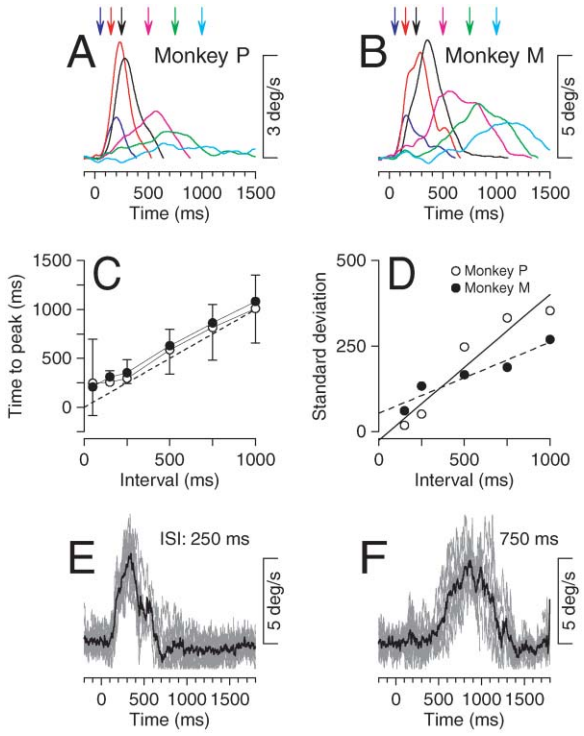

Figure 2. Learned Timing in the Pursuit System

(A and B) Learned vertical eye velocity is plotted as a function of time for experiments that used learning trials with changes in target direction after ISIs of different durations. Each color corresponds to a different ISI, and the time at which the target changed direction in the learning trials is indicated by the downward arrows. (C) Time to the peak of the learned vertical eye velocity is plotted as a function of the ISI. Error bars give standard deviations for means measured from individual trials. (D) Standard deviation of the time to the peak learned vertical eye velocity is plotted as a function of the ISI. In (C) and (D), open and filled symbols show results for monkeys P and M. (E and F) Examples of learned responses for two different values of ISI. Black traces show the average learned vertical eye velocity, and gray traces show the ten sample individual trials that comprise the average. In (E) and (F), values of ISI were 250 and 750 ms.

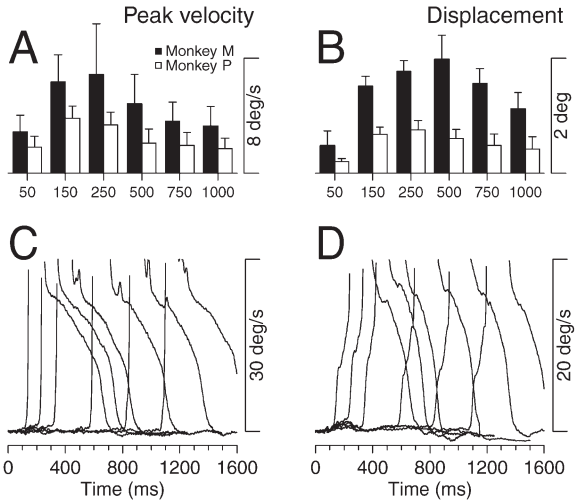

Figure 3. Relationship between the Size of the Learned Vertical Eye Movement and the ISI

(A) Each bar shows the average peak of the learned vertical eye velocity at a particular ISI. (B) The bars show the average total displacement of vertical eye position in the postlearning probe trials, again as a function of ISI. In (A) and (B), filled and open bars show data for monkeys M and P. (C and D) Average vertical eye velocity during the first ten learning trials as a function of the time from the onset of the initial horizontal target motion for monkeys M and P, respectively. Different traces show eye velocity during learning trials with different values of ISI.

was 1000 ms (Figure 2D). Regression analysis supported a linear relationship between the standard deviation in the time to peak of the learned eye movement and the value of ISI. The linear relationship is consistent with Weber's law, which in the timing literature has been taken to mean that the variability estimating the passage of time should be proportional to the interval being estimated (Gibbon et al., 1997).

The eye movements in the postlearning probe trials are complicated by the presence of visual feedback. As soon as the learned vertical smooth eye movement begins, vertical eye velocity is driven away from vertical target velocity, which is zero in the probe trials. The resulting image motion in the opposite direction should provide a drive to return vertical eye velocity to zero. Due to the intrinsic visual delay in the pursuit system, we might expect the peak velocity of the learned vertical eye movement to occur at the time the delay expires, about 100 ms after the onset of the eye movement (Lisberger et al., 1987). However, inspection of the average traces in Figures 2A–2B belies this logic, as the interval from the onset of the learned eye movement to its peak can be as long as 400–500 ms. Figures 2E and 2F plot ten individual learned eye movements from monkey M (gray traces) and their average (black trace) and confirm that the durations of the average responses plotted in Figures 2A and 2B provide an accurate reflection of the durations of the responses in individual trials. These results demonstrate that the time to peak vertical eye velocity in the probe trials is not correlated with the onset of the learned eye movement; instead, as shown in Figure 2C, visual feedback starts to drive image motion back toward zero approximately 100 ms after the expected change in target motion does not occur.

To quantify the relationship between the amplitude of the learned response and the ISI, Figure 3A plots the mean and standard deviation of the peak vertical velocity of the learned eye movements. Data were averaged across several experimental days at each value of ISI. For both monkeys (open and filled bars), the relationship between peak learned response and ISI shows an inverted-U shape. The largest values of learned vertical eye velocity occurred for intermediate values of ISI; smaller amplitudes were obtained with the shortest (50 ms) or longest (1000 ms) values of ISI. A similar inverted-U function characterizes the relationship between learned response and ISI when we compute the area under each vertical eye velocity trace to report the total upward displacement in the learned eye movement (Figure 3B). Note that for this analysis we computed the displacement after removing saccades from the raw position traces because we wanted to look at the smooth pursuit system in isolation, without any potential contributions from the saccadic system.

We next examined whether the average amplitude of the learned eye movement for a particular ISI was correlated with the average performance during the learning trials. The traces in Figures 3C and 3D show that the vertical eye velocity evoked during the first ten learning trials did not depend on the ISI. Each response began with an early saccade shortly after the onset of upward target motion, shown by the gaps in vertical eye velocity near the start of each trace. The saccade was followed by smooth eye velocity responses to the 500 ms pulse of vertical target velocity. Neither the onset latency, size, or duration of the initial saccade nor the amplitude of the subsequent upward pursuit velocity varied significantly as a function of ISI for monkey M or P (Figures 3C and 3D, respectively). Because the response to the vertical target motion during the initial learning trials was the same for all values of ISI, we conclude that performance deficits cannot be responsible for the effect of ISI on the size of the learned response.

Having established that learned eye movements are temporally specific for the particular ISI used in the learning trials, the next two sections examine how the different motion signals that are available during a typical pursuit trial contribute to the timing of the learned eye movement.

Contribution of Positional Signals to Learned Timing

In each experiment presented so far, the onset of vertical target motion in the learning trials always occurred at a fixed location on the screen. We used the experiment diagrammed at the top of Figure 4 to test whether the pursuit system was determining when to trigger the learned eye movement simply by learning the location of the change in target direction. On learning trials, rightward target motion at 10°/s began 5° to the right of center. After 500 ms of horizontal target motion, when the target reached 10° to the right of center, a component of vertical target motion was added (Figure 4, top left icon). In the postlearning probe trials (Figure 4, top right five icons), target motion was purely horizontal, and we varied the initial fixation position so that, after the 500 ms ISI expired, the target was at a different position on the screen for each probe trial. Depending on whether the position or the time of the change in target direction were being learned, the peak vertical velocity of the learned eye movement should occur at either the same position (10° to the right) or the same time (500 ms after the onset of target motion), independent of the initial target position in the probe trial.

As shown in Figure 4, in both monkeys, the learned eye movement occurred *when* rather than *where* the target changed direction in the learning trials. When the learned vertical eye velocity for different probe trials is averaged separately and plotted as a function of the horizontal position of the target (Figures 4A and 4B), the traces show peaks at different positions. In contrast, when the same data are plotted as a function of time from the onset of target motion, all the traces show peaks at about the same time (Figures 4C and 4D). Varying the initial position for the probe target did affect the size of the learned response; amplitude declined as a function of the difference between the initial target position in the probe and learning trials.

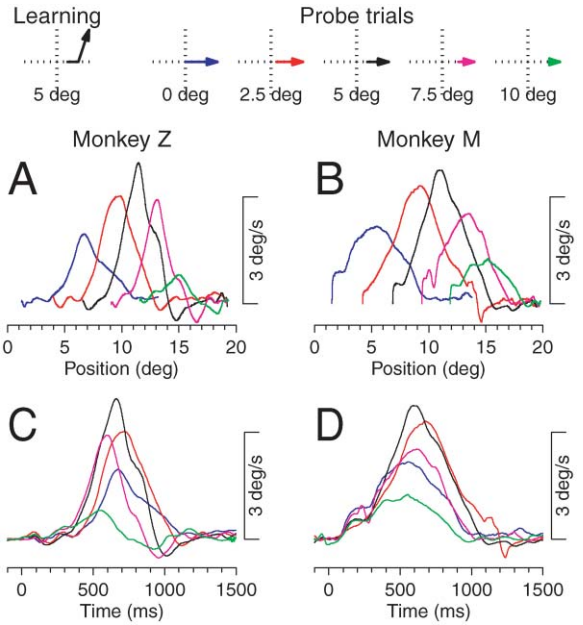

Figure 4. Demonstration that the Pursuit System Learns the Time but Not the Position of the Change in Target Direction

The leftmost icon shows the target motion in the learning trials in terms of horizontal and vertical position on the screen; targets started 5° to the right and moved at 10°/s for 500 ms before changing direction. The righthand five icons show the target motion in the probe trials; targets started 0°, 2.5°, 5°, 7.5°, or 10° to the right of center and moved rightward at 10°/s. In both sets of icons and in the eye velocity traces in (A)–(D), the colors indicate the different initial horizontal positions of the probe trials. (A and B) Averages of learned vertical eye velocity are plotted as a function of horizontal target location on the screen. (C and D) The same averages of learned vertical eye velocity are plotted as a function of time since the onset of horizontal target motion. (A) and (C) show data from monkey Z; (B) and (D) show data from monkey M.

Figures 5A and 5B summarize the data for this experiment by plotting the horizontal target position as a function of the time at the peak of the learned vertical eye velocity in each individual postlearning probe trial. Different colors have been used to represent the data for the different initial positions in the probe trials. Each set of colored points plots along a diagonal line with a slope equal to the speed of the target (i.e., 10°/s), because time and horizontal position proceed in lock-step as the target moves horizontally at constant speed from a given initial position. The data for each set of probe trials with a particular initial target position have been summarized by a rectangle that is centered at the median values of position and time and whose sides are one standard deviation in length. When rectangles for different sets of colored points overlapped, they were joined to form a polygon. The rectangles for different probe trials should be aligned vertically or horizontally depending on whether the pursuit system had learned the time or the position of the change in target direction. For the experiment shown in Figure 4, when the change in target motion in the learning trials always occurred at the same location and at the same time, the data for probe trials

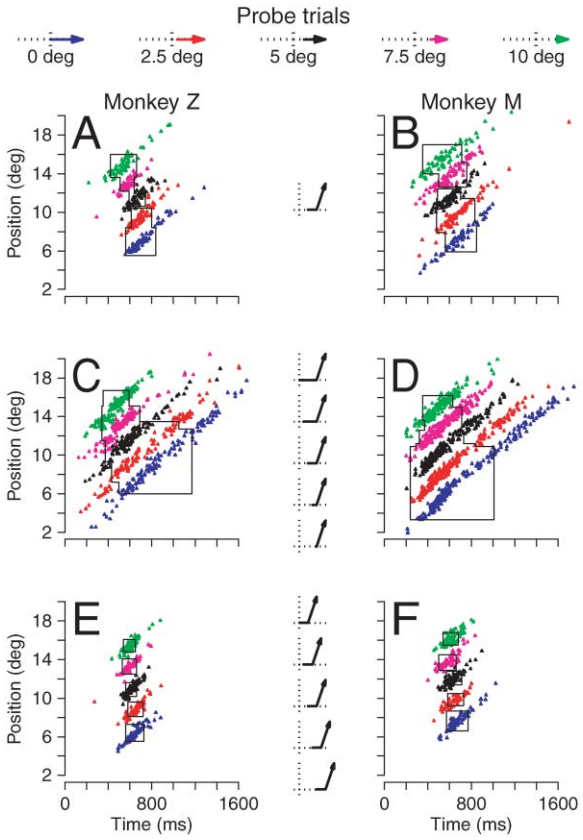

Figure 5. Quantitative Assessment of Whether the Pursuit System Learns Time or Position under Different Conditions

Each symbol shows the results from one probe trial and plots the horizontal position of the peak learned eye velocity as a function of the time of the peak; each color shows data for probe trials that started at one of the five different horizontal positions (as indicated in the top row of icons). Polygons were formed by merging overlapping rectangles, each rectangle centered at the median position and time for all the probe trials starting at a particular horizontal position. The side of each of the five rectangles has a length equal to one standard deviation along each axis. (A and B) Conditions allowed learning either the horizontal position or the time of the change in target direction. In learning trials, the target moved rightward at 10°/s beginning 5° to the right, and the change in target motion always occurred at the same time (500 ms after target onset) and the same location on the screen (10° to the right). (C and D) Conditions attempted to force learning the position of the change in target direction. In the learning trials, targets moved rightward at 10°/s beginning 0°, 2.5°, 5°, 7.5°, or 10° to the right, and the change in direction occurred 1000, 750, 500, 250, and 0 ms after the onset of target motion, always at a position 10° to the right. (E and F) Conditions attempted to force learning the time of the change in target direction. In the learning trials, targets moved rightward at 10°/s beginning 0°, 2.5°, 5°, 7.5°, or 10° to the right, and the change in direction always occurred 500 ms after the onset of target motion, when the target was located 5°, 7.5°, 10°, 12.5°, and 15° to the right of the center of the screen. The icons in the center of the figure summarize the target motions used in the learning trials of the three different experiments.

starting at different positions aligned in a vertical column (Figures 5A and 5B), indicating that the peak vertical velocity of the individual learned eye movements occurred at the same time but different positions.

We next asked whether we could force the pursuit system to learn the position of a change in the direction of target motion. In the experiment diagrammed in the icons between Figures 5C and 5D, initial target position differed across learning trials so that the onset of vertical target motion occurred at a time that was not reliable, but always at the same horizontal position on the screen (i.e., 10° to the right of center). The probe trials were the same as those in Figure 4. The peak vertical velocity of the learned eye movement occurred over a wide range of times and positions in different probe trials and gave little evidence of the horizontal orientation of the data that would be expected if the pursuit system had successfully learned the position of the change in target direction (Figures 5C and 5D). Statistical evaluation using Levene's test for homogeneity of variance verified that the pursuit system had not learned position: the variability in target position at the time of the peak learned eye velocity was the same or larger in Figures 5C and 5D than in Figures 5A and 5B. In a final set of experiments (diagrammed in the icons between Figures 5E and 5F), the change in target direction occurred over a range of positions on the screen but always after the same duration of horizontal motion (i.e., 500 ms), forcing the system to learn time rather than position. The probe trials again were the same as those in Figure 4. The peak vertical velocity of the learned eye movement in different probe trials plotted very close to the vertical stack that would be expected if the pursuit system had learned the time of the change in target direction (Figures 5E and 5F). We conclude that for this set of experiments, target position on the screen is not, and cannot, be used to learn the time of a change in the direction of target motion.

Contribution of Distance- and Time-Related Signals to Learned Timing

In the experiments shown so far, the pursuit system might have learned when the target would change direction by measuring the duration of the ISI or the horizontal distance traversed by the target during the ISI. To test whether the pursuit system was learning the time of the change in target direction or the horizontal distance that the target moved before the change in direction occurred, we disrupted the fixed relationship between time and distance at a given speed by varying horizontal target speed. First, we varied horizontal target speed only in the probe trials (Figure 6) and in the last two experiments (Figure 7) to force the pursuit system to learn either time or distance, in both learning and probe trials.

In the experiment presented in Figure 6, there was only one type of learning trial (top left icon). The target started by moving horizontally at 10°/s. It always changed direction after a fixed time of 500 ms had elapsed and a fixed distance of 5° had been traversed. In the postlearning probe trials, we varied the horizontal target speed to dissociate time and distance, just as we had varied initial target position to dissociate time and position in Figure 4. Depending on whether distance or time were being learned, the vertical velocity of the learned eye movement would be expected to reach a peak when the target had either (1) traversed the same horizontal distance (5°) or (2) moved for the same amount of time after the

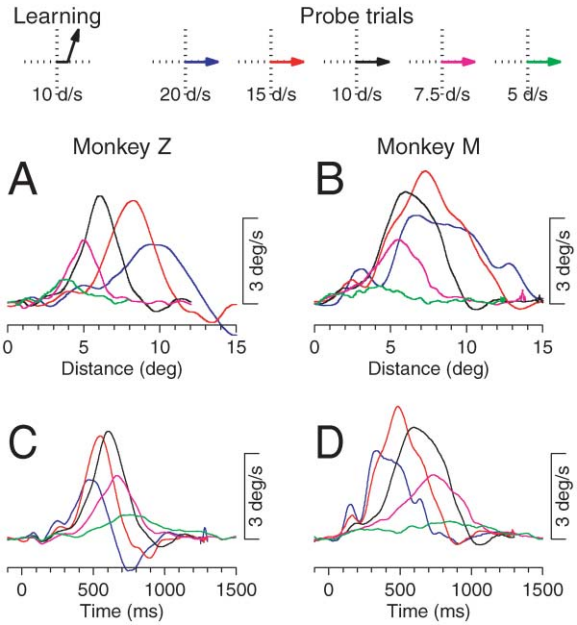

Figure 6. Demonstration that the Pursuit System Learns an Intermediate between Time and Distance When Both Signals Are Equally Reliable Predictors of the Change in Target Direction

The leftmost icon shows the target motion in the learning trials in terms of horizontal and vertical position on the screen; targets started at the center of the screen and moved at 10°/s for 500 ms before changing direction. The righthand five icons show the target motion in the probe trials; targets started at the center and moved rightward at 20°, 15°, 10°, 7.5°, or 5°/s. In both sets of icons and in the eye velocity traces in (A)–(D), the colors indicate the different horizontal speeds of the probe trials. (A and B) Averages of learned vertical eye velocity are plotted as a function of the horizontal distance traveled by the target. (C and D) The same averages of learned vertical eye velocity are plotted as a function of time from the onset of horizontal target motion. (A) and (C) show data from monkey Z; (B) and (D) show data from monkey M.

onset of target motion (500 ms), independent of the target speed in the probe trial. Figure 6 shows that when the learned vertical eye velocity for the different probe trials is averaged separately, the peaks of the average traces did not align perfectly when plotted as a function of either horizontal distance (Figures 6A and 6B) or time (Figures 6C and 6D). For monkey Z, the peaks of the learned vertical eye velocity traces aligned better when plotted as a function of time, indicating that for the most part the pursuit system learned that the change in target direction would occur 500 ms after motion onset. For monkey M, the opposite was true; the peaks aligned better when plotted as a function of horizontal distance, indicating that for the most part the pursuit system learned that the change in target direction would occur after the target had moved 5°.

In the final two experiments, we varied horizontal target speed in the learning trials of each daily experiment to ask whether the pursuit system could be forced to learn either the time of the change in target direction or the distance that the target had to move before this change occurred. To promote learning of time, all learning trials had the same value of ISI (500 ms), but we varied horizontal target speed so that the target traversed different distances during the ISI (five icons at the top of Figure 7A). As was done for the experiment shown in Figure 6, probe trials were presented at different velocities. For both monkeys, the peaks of the average vertical eye velocity traces for the different probe trials were better aligned when plotted as a function of time (Figures 7A3 and 7A4) than when they were plotted as a function of horizontal distance (Figures 7A1 and 7A2).

In the experiment in Figure 7B, we promoted learning of distance by varying systematically the ISI and the horizontal target speed in different learning trials so that the target always traversed the same horizontal distance of 5° during the ISI (five icons at the top of Figure 7B). As in Figures 6 and 7A, probe trials delivered different target velocities. When the learned vertical eye velocity for different probe trials was averaged separately and plotted as a function of the horizontal distance traversed by the probe target, the peaks of the average traces were aligned better than they had been in Figure 7A, although the alignment was not perfect (Figures 7B1 and 7B2). However, the peaks were very poorly aligned when the same average vertical eye velocity traces were plotted as a function of time (Figures 7B3 and 7B4). For both sets of experiments in Figure 7, the peak vertical velocity of the learned eye movement was larger when the probe target moved at higher speeds, even though all target velocities were represented equally in the learning trials.

Figure 8 summarizes the data from the three time-versus-distance experiments presented in this section in the same way that Figure 5 summarized the time-versus-position experiments. The data should stack vertically or horizontally depending on whether time or distance, respectively, had been learned. When the pursuit system was unconstrained because the learning trials provided target motion at only one speed, probe trials of different speeds plotted obliquely, indicating that a combination of distance and time had been learned (Figures 8A and 8B). When the learning trials provided target motions of different speeds that changed direction after the same ISI but different distances, the data plotted vertically, indicating that time had been learned (Figures 8C and 8D). Finally, when the target motion on learning trials changed direction after traversing a constant distance but different ISIs, the data plotted horizontally, indicating that distance had been learned (Figures 8E and 8F). Statistical analysis using Levene's test for homogeneity of variance demonstrated that for both monkeys the variability in the time of the peak learned eye velocity was lower in Figures 8C and 8D, whereas the variability in the distance traveled at the time of the peak learned eye velocity was lower in Figures 8E and 8F ($p < 0.01$). We conclude that the pursuit system determines when to emit a learned eye movement by keeping track of elapsed time and distance traveled by the target and that the relative contributions that these two signals make to motor timing can be influenced by the conditions in the learning trials.

Discussion

Representation of Time for Motor Control

We have found that the pursuit system can learn to emit a response that is timed to the occurrence of an

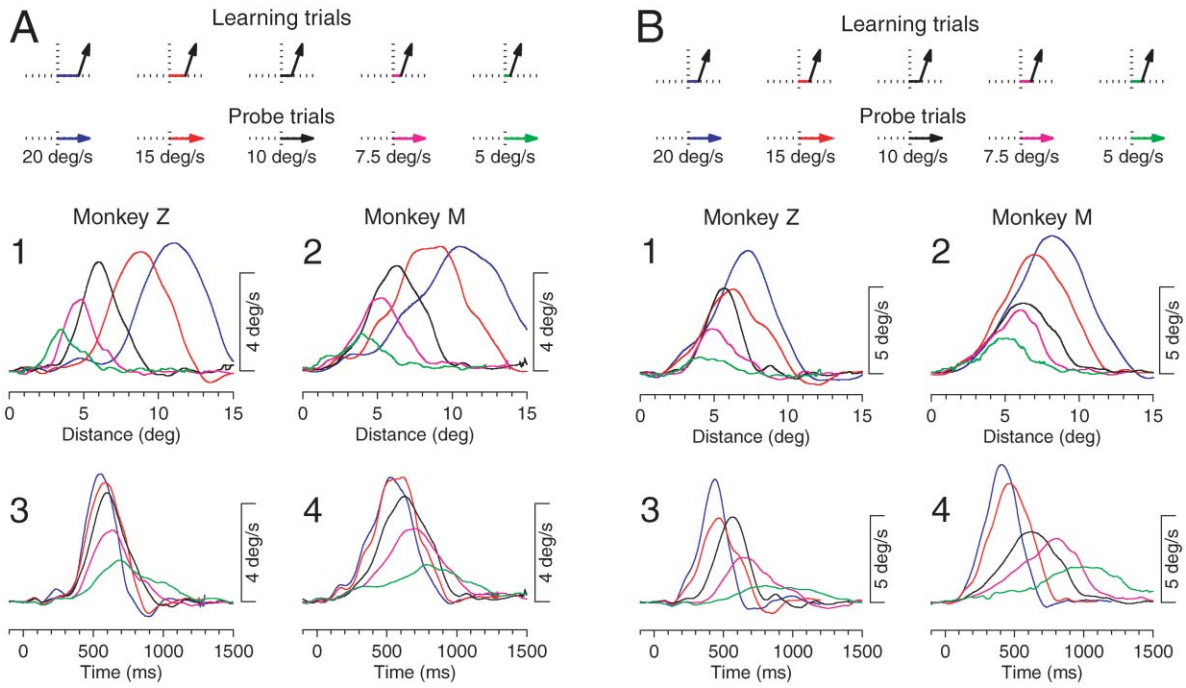

Figure 7. Average Learned Eye Velocity Records Showing that the Conditions in the Learning Trials Can Influence Whether the Pursuit System Learns the Duration of the ISI or the Distance Moved by the Target during the ISI

In the top row, the two sets of five icons show target motion in the learning trials. The horizontal speed in the probe trials was varied as in Figure 6 and is indicated by the different colors in the learned eye velocity traces in (A) and (B). (A) Conditions designed to promote learning the time of the change in target direction. On learning trials, targets started at the center of the screen and moved to the right at speeds of 20°, 15°, 10°, 7.5°, and 5°/s for 500 ms, traversing 10°, 7.5°, 5°, 3.75°, and 2.5° before undergoing a change in direction. (B) Conditions designed to promote learning the horizontal distance moved by the target before the change in direction. On learning trials, targets started at the center of the screen and moved to the right at speeds of 20°, 15°, 10°, 7.5°, and 5°/s; the value of ISI was 250, 333, 500, 666, and 1000 ms so that the change in target direction always occurred after the target had moved 5°. (A1, A2, B1, and B2) Averages of learned eye velocity are plotted as a function of the horizontal distance that the target had moved. (A3, A4, B3, and B4) The same averages of learned eye velocity are plotted as a function of time from the onset of horizontal target motion.

expected change in target direction and that this temporal precision can be achieved explicitly, by measuring the duration of a time interval, and implicitly, by keeping track of the distance a target has traveled. Our findings provide a counterexample to the suggestion that the adaptation of visually guided movements may be unable to employ an explicit representation of time (Karniel and Mussa-Ivaldi, 2003). Further, our findings seem to contradict a recent hypothesis that the neural circuits representing time explicitly might be separate from those that make use of motion signals to keep track of the passage of time (Lewis and Miall, 2003). Instead, our results demonstrate that the neural circuitry driving smooth pursuit in primates has access to both time and distance cues, and it appears that these two signals are used concurrently to guide learned timing.

Prior research has provided abundant examples of explicit and implicit representations of time for motor control. Other evidence for an explicit representation of time has come from (1) interval discrimination tasks that require the subjects to discriminate which of two consecutive stimuli is longer in duration (Buonomano and Karmarkar, 2002; Wright et al., 1997), (2) conditioning tasks that require the subjects to generate a response at a particular time after the presentation of a cue, either for positive reinforcement or to avoid a harmful stimulus (Gallistel and Gibbon, 2000; Gibbon et al., 1997; Mauk and Ruiz, 1992), and (3) tapping tasks that require the subjects to synchronize finger movements with the beat of a metronome (Spencer et al., 2003; Wing, 2002). Examples in which time is computed implicitly from signals with temporal structure include (1) continuous drawing tasks, where temporal consistency can be achieved by keeping the angular velocity of a circular movement constant, without measuring time explicitly (Killeen and Weiss, 1987; Spencer et al., 2003), (2) "time-to-collision" tasks, where subjects use signals related to the speed, distance, or looming of a moving object to estimate the time until it reaches a designated location (Regan and Gray, 2000; Sun and Frost, 1998; Tresilian, 1999), and (3) throwing following prism adaptation (Martin et al., 2001). Our results demonstrate that one behavioral system can encode the passage of time either explicitly or implicitly depending on task conditions.

To determine when to emit the learned eye movement using information related to the distance traveled by the target, the pursuit system could capitalize on the identity: target speed equals distance traveled divided by the duration of motion. Target speed is a signal that is readily available from the visual system when the eye is stationary and is equal to the eye speed represented in the cerebellum (Lisberger and Fuchs, 1978; Miles et

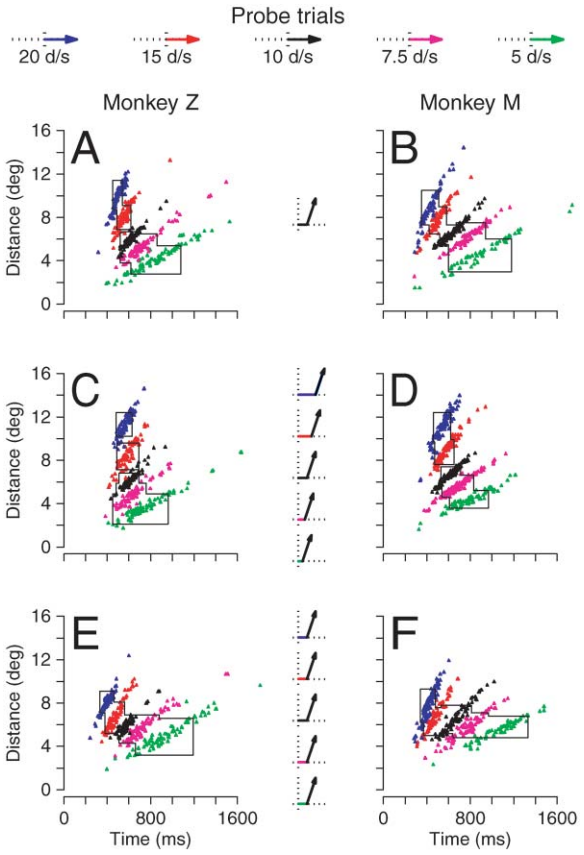

Figure 8. Quantitative Assessment of Whether the Pursuit System Learns Time or Distance under Different Conditions

Each symbol shows the results from one probe trial and plots the horizontal distance the target had moved at the peak of the learned eye velocity as a function of the time of the peak; different colors show data for probe trials of different horizontal speeds (as indicated in the top row of icons). Polygons were formed by merging overlapping rectangles, each rectangle centered at the median distance and time for all the probe trials using a particular horizontal speed. The side of each of the five rectangles has a length equal to one standard deviation along each axis. (A and B) Conditions allowed learning of either distance or time by changing the direction of the target at a constant time after motion onset and after the target had moved a constant distance. (C and D) Conditions attempted to force the pursuit system to learn the time of the change in target direction. In the learning trials, the target changed direction after it had moved different distances, but at a constant time after the onset of motion. (E and F) Conditions attempted to force the pursuit system to learn how far the target would move before changing direction. In the learning trials, the target changed direction at different times after motion onset but after it had moved a constant distance. The icons in the center of the graph summarize the target motions used in the learning trials.

al., 1980) and cortical areas MST (Newsome et al., 1988; Sakata et al., 1983) and FPA (Fukushima et al., 2000; Gottlieb et al., 1994) when tracking is accurate. Distance could be computed by taking the time integral of speed using neural mechanisms like those proposed for the oculomotor velocity-to-position integrator (Robinson, 1989; Seung et al., 2000) and for the accumulation of evidence for perceptual decisions (Durstewitz, 2003; Mazurek et al., 2003; Wang, 2002). Given the relationship among speed, distance, and time, it seems natural for the pursuit system to use any or all of these signals to keep track of time. In contrast, target position is not one of the signals that naturally drives smooth pursuit as indicated, for example, by the observation that step-ramp target motion causes pursuit to be initiated in the direction of the target motion, not in the direction of the step in position (Rashbass, 1961). Our finding that target position cannot be used by the pursuit system to represent time suggests that different movement systems probably use different signals to keep track of time, perhaps drawing from the signals that are part of their natural repertoire.

Although there is a sense in which pursuit learning in the paradigm used here may be similar to anticipatory or predictive pursuit of periodic target motions (Barnes and Asselman, 1991; Vandenberg, 1988), we remain cautious about extending our conclusions to all predictive and anticipatory pursuit behaviors. Pursuit learning appears to be localized in subcortical structures (Chou and Lisberger, 2004; Kahlon and Lisberger, 2000), whereas anticipatory pursuit depends on cognitive expectations (Kowler, 1989), engages the cerebral cortex (Heinen and Liu, 1997), and is partially spared after cerebellar lesions (Waterston et al., 1992). Until the neural signals and the cellular mechanisms responsible for these various phenomena have been elucidated, however, it is difficult to come to any firm conclusions about the degree to which our findings for pursuit learning in a stimulus-response situation will be applicable to the timing of anticipatory smooth pursuit eye movements in other tasks.

Factors Affecting the Amplitude of the Learned Eye Movement

The variations in learning conditions used here had a number of interesting effects on the amplitude of the learned eye movement. First, when learning was probed with targets that started at different positions on the screen, the amplitude of the learned response was largest for the starting position used in the learning trials and decreased as the initial target position was moved away. Second, when learning was probed with target motion of different speeds, the amplitude of the learned response increased as a function of speed. Third, the amplitude of learning depended on the interval between the onset of horizontal and vertical target motion, showing the largest learned response for values of ISI between 150 and 500 ms, with smaller (but properly timed) responses for longer or shorter values of ISI. Control analyses showed that the effect of ISI on the amplitude of learning cannot be due to a "performance" deficit attributed to differences in the eye movements evoked after the target changed direction in the different learning trials.

We can offer explanations for each of these three observations in the context of pre-existing concepts of learning and smooth pursuit eye movements. In theories of generalization, the expression of learning for any given particular probe stimulus depends on how much the neural representation of the probe stimulus overlaps with that of the learning stimulus (Mclaren and Mackintosh, 2002). Our results for changes in the initial target position of probe trials conform to the classical general-

ization effect and would be expected if the representation of probe target motions starting from different positions overlapped by an amount that decreased as a function of the distance between the starting positions of the learning and probe motions. The effect of the speed of the probe stimulus on the amplitude of learning may be related to the prior demonstration of a variable gain control within the visual-motor transformations for pursuit (Schwartz and Lisberger, 1994). Since the setting of the gain control is a function of target speed (Schwartz and Lisberger, 1994), higher values of internal gain for higher target speeds could explain a larger expression of learning and might even obscure a classical generalization effect for target speed.

Finally, to explain the relationship between the size of the learned response and the ISI, we suggest that there is an "eligibility trace" for pursuit learning (Sutton and Barto, 1981). When the eligibility trace is large, then learning can occur at that time; if it is small or absent, then learning is poor even though motor performance might be excellent at the time. To explain our data, we propose that an eligibility trace is triggered by the onset of target motion, peaks at about 150–250 ms later, and then declines gradually. Our data do not indicate whether the time course of the eligibility trace for pursuit learning results from the timing requirements of the cellular and molecular mechanisms responsible for learning or from the timing of the neural signals that guide learning. However, we favor an important role for the neural signals themselves, because the duration of the eligibility trace is long relative to the timing requirements of putative cellular mechanisms of learning such as spike timing-dependent plasticity (Bi and Poo, 1998) or even of cerebellar long-term depression (Chen and Thompson, 1995; Wang et al., 2000).

Is Pursuit a Form of Cerebellar Learning?

Although a large number of neural systems have been implicated in the representation of time for different tasks (Lewis and Miall, 2003), we favor the hypothesis that the cerebellum plays a key role in learned timing for smooth pursuit eye movements. The cerebellum is required for accurate smooth pursuit eye movements (Robinson and Fuchs, 2001), and recordings from Purkinje cells in the floccular complex of the monkey's cerebellum have shown that their firing changes in directions and amounts that would be appropriate to drive the learned eye movement (Kahlon and Lisberger, 2000). The cerebellum has also been implicated in learning of smooth pursuit movements to targets with periodic trajectories (Suh et al., 2000). Our demonstration that learned eye movements are temporally specific and the long-standing idea that the cerebellum is important for temporal processing provide additional reasons to think there may be a link between the cerebellum and learned timing for pursuit. One idea about the representation of time in the cerebellum posits that synchronicity in its climbing fiber input at very precise moments of a movement can act as a neural clock to provide an explicit representation of time (Welsh et al., 1995). However, our finding that both explicit and implicit temporal cues contribute to learned timing suggests that a broader set of neural mechanisms work together. If the cerebellum is the site where time is kept for pursuit learning, then an important contribution almost certainly is made by the eye velocity and image motion signals transmitted by mossy fiber inputs, which could be used to derive an implicit representation of the passage of time (Miles et al., 1980).

Finally, the temporal requirements for pursuit learning bear a striking resemblance to those exhibited in a variety of cerebellar-dependent learning tasks, including adaptation of saccadic eye movements (Shafer et al., 2000), motor learning in the vestibulo-ocular reflex (Raymond and Lisberger, 1998), and classical conditioning of the eyelid response (Schneiderman and Gormezano, 1964). Thus, it is tempting to think that an eligibility trace with a peak in the 150–250 range and a duration of 1–2 s will be a feature of all cerebellar-dependent forms of learning, including those related to the involvement of the cerebellum in nonmotor tasks. Furthermore, the remarkable similarity of the learning and the involvement of the cerebellum in each of these behaviors suggest that learned timing may be mediated by a shared set of circuit and cellular mechanisms.

Experimental Procedures

Animals

Three rhesus monkeys (*Macaca mulatta*) served as subjects. Two (monkeys M and P) had participated in previous studies of pursuit learning where double steps of target speed were used to cause a learned increase or decrease in eye speed during the initiation of pursuit (Kahlon and Lisberger, 1996), but all three were naive to the directional learning paradigm used here. Monkey P showed only small learned eye movements with ISIs longer than 500 ms and did not participate in the experiments of Figures 4–8. To instrument them for experiments, each monkey was anesthetized with isofluorane, and a search coil was implanted on one eye so that eye position could be measured using the magnetic search coil technique (Judge et al., 1980). Custom-cut orthopedic stainless steel strips were attached to the monkeys' skull with 8 mm long screws. The straps served as the foundation for dental acrylic to secure a receptacle that was used to fix the head to the primate chair. Appropriate analgesic and antibiotic treatments were administered postoperatively. After recovery from surgery, monkeys were trained to sit in a primate chair with the head restrained and to fixate and track spots of light that moved across an analog oscilloscope placed in front of them. All procedures involving the monkeys had been approved in advance by the *Institutional Animal Care and Use Committee* at UCSF.

Pursuit Targets and Data Acquisition

Targets were presented on an analog oscilloscope (Hewlett Packard 1304a) and appeared as bright 0.4° squares on a dark background. The display was driven by a digital signal processing board with 16 bit digital-to-analog converters, creating a nominal spatial resolution of 65,536 × 65,536 pixels and a temporal resolution of 4 ms. The display was positioned 30 cm in front of the monkey and subtended 48 × 38° of visual angle. All experiments were carried out in a dimly lit room. Sequences of target motion were controlled by a combination of DEC Alpha UNIX workstations, which provided a user interface for programming and modifying the particular target motion sequence to be presented, and PC/Windows NT machines, which performed all the real-time operations and controlled the visual displays. Signals proportional to horizontal and vertical eye position were passed through an analog circuit to create signals proportional to horizontal and vertical eye velocity. The circuit differentiated frequency content from 0 to 25 Hz and filtered higher frequencies with a roll-off of 20 db/decade. These analog signals were digitized at 1000 samples/s and stored for analysis.

Experimental Design

Before each daily experiment, the eye coil was calibrated by holding the target stationary at known positions and rewarding the monkey for fixating the target with the head fixed. Experiments consisted of a series of trials, each lasting ~2 s. At the start of each trial, a stationary target appeared and monkeys were required to fixate within a $2^\circ \times 2^\circ$ window for an interval that was randomized between 600 and 1200 ms. To minimize the occurrence of saccades during the initiation of pursuit, initial target trajectories followed the standard step/ramp paradigm (Rashbass, 1961); after the fixation period, the target was displaced horizontally eccentric to the position of gaze (step), and immediately began moving toward the fixation point (ramp). The size of the step depended on the monkey as well as the subsequent speed of the ramp. Note that in order to avoid clutter, the step in position has been omitted from the icons in the figures. The monkeys were allowed 250 ms to bring their gaze within a $2^\circ \times 2^\circ$ window centered on the moving target. This window was opened to $5^\circ \times 5^\circ$ during probe trials, and for 250 ms following the change in target direction during the learning trials. If the monkeys kept gaze within the window as long as the target was visible, then they received a fluid reinforcement at the end of the trial. The initial fixation target usually appeared at straight ahead gaze. In some experiments, however, we adjusted the location of the fixation target on the screen but retained the basic target trajectory of a step in one direction followed by a ramp of target motion in the opposite direction.

Each daily experiment started with a prelearning baseline block of trials, immediately followed by the learning block. The baseline block consisted of 50 to 100 trials in which the target moved to the left and an equal number of randomly interleaved trials in which the target moved to the right. This block is necessary so that a learned eye movement can be later calculated by subtracting the vertical eye velocity in each of the probe trials of the learning block from the average vertical eye velocity in the same type of trials of the prelearning baseline block. The learning block, which followed immediately after the baseline block, contained the following trials (randomly interleaved): (1) approximately 500 learning trials in which the target moved in one of the horizontal directions (i.e., the learning direction) for a predesignated interval before changing direction by the addition of a vertical component of target motion, (2) 50 to 100 probe trials in which learning was assessed by having the target move as in the learning trials but not change direction, and (3) approximately 500 control trials in which the target simply moved horizontally, opposite to the learning direction. These control trials were included to counterbalance the number of trials in which the target moved in the learning direction and thus prevent the monkeys from anticipating target motion. In the majority of the experiments, the interval of time between the onset of target motion and the change in target direction in the learning trials was kept constant for the whole day, although it was varied from one daily experiment to the next. Variations on this theme, as well as the exact blend of initial target positions and speeds of motion, were customized for different experiments in ways that are described at the relevant site in the Results.

Data Analysis

Eye velocity data were analyzed after each experiment on a DEC Alpha UNIX workstation using an interactive computer program. The horizontal and vertical eye velocity traces from individual trials were displayed on the computer screen, and saccades were removed from averaged data using two different methods. In one, we used the cursor to point out the start and end of each rapid deflection of eye velocity and replace it with a line segment that connected the eye velocities before and after the excision. In the second method, we excised the saccade as before, but treated the excised interval as missing data during averaging. Because the two methods provided virtually identical results, the figures only present traces obtained using the first approach. It is necessary to remove saccades to isolate and analyze the pursuit component of eye velocity, but the effects of learning that we observed were large and could be neither produced nor obscured by any reasonable method of dealing with saccades (Churchland and Lisberger, 2001). After saccades had been excised from individual trials, eye velocity traces were aligned on the onset of target motion, averaged, and filtered with a 25 Hz digital filter. The filter reduced noise without noticeable effects on the basic trajectories of the traces. For each postlearning probe trial of a particular type, we computed a learned eye velocity response by subtracting the average vertical eye velocity in the prelearning trials of the same type from the vertical eye velocity in the individual postlearning probe trial.

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